VARIATION AND SPECIATION IN THE GENUS *HUDSONIA*[1]

JUDITH TROOP SKOG[2] AND NORTON H. NICKERSON[3]

ABSTRACT

Study of herbarium specimens and of living populations of *Hudsonia* plants over several seasons showed a wider range of variation than could be accommodated by the present nomenclature of the genus. Four characters (leaf length, pedicel length, leaf hairiness, and ovary hairiness) were found to form distinct associations on a scatter diagram. Ecological conditions showed correlations with these morphological associations. The associations are designated as five subspecies of *Hudsonia ericoides* L. Linnaeus' type specimen of the genus is a taxon intermediate between subsp. *tomentosa* and an unnamed clearly distinct taxon now apparently confined to Nova Scotia but formerly more widespread southward along the coast. This latter heretofore unrecognized taxon is here described as *H. ericoides* subsp. *andersonii*. Evidence is presented which indicates that this subspecies is headed toward oblivion by man's use of its habitat.

Representatives of the genus *Hudsonia* collected from 1963 to 1965 at many stations along the coast of New England were found to vary from the descriptions given in *Gray's Manual of Botany, 8th Edition* (Fernald, 1950) for either *H. ericoides* L. or *H. tomentosa* Nutt. Inclusion of these specimens in *H. tomentosa* var. *intermedia* Peck made the morphogical limits of that taxon extremely wide. Fernald further noted that this variety "needs critical study," and that it "resembles a hybrid between *H. ericoides* and *H. tomentosa*." Hall (1956) concluded that the var. *intermedia* Peck was a backcross from hybridization or is an introgressant. This study presents evidence for a much wider range of character variation and proposes the nomenclatorial changes demanded.

METHODS

Both herbarium specimens and living populations of the genus *Hudsonia* were studied. Voucher specimens of these populations are deposited in the Tufts University Herbarium, Medford, Massachusetts. Collections were examined from the following herbaria: ACAD, BH, CONN, DAO, FLAS, GH, MO, NCU, NEBC, NHA, NY, US, and Tufts University. Population samples from Massachusetts, New Hampshire, Maine, and Nova Scotia were measured for five morphological characters: degree of hirsuteness of leaves, degree of hirsuteness of ovaries, lengths of leaves, lengths of pedicels, and number of seeds per fruit. A scale of increasing hairiness from 1 to 5 was used for the first two measurements; lengths to the nearest 0.5 mm were measured with a standard laboratory ruler for the next two. For individual plants, an average of 10 values for each measurement was taken. These values, from both living and preserved specimens, were plotted on a pictorialized scatter diagram

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[2] Department of Biology, George Mason College of the University of Virginia, Fairfax, Virginia 22030.

[3] Department of Biology, Tufts University, Medford, Massachusetts 02155.

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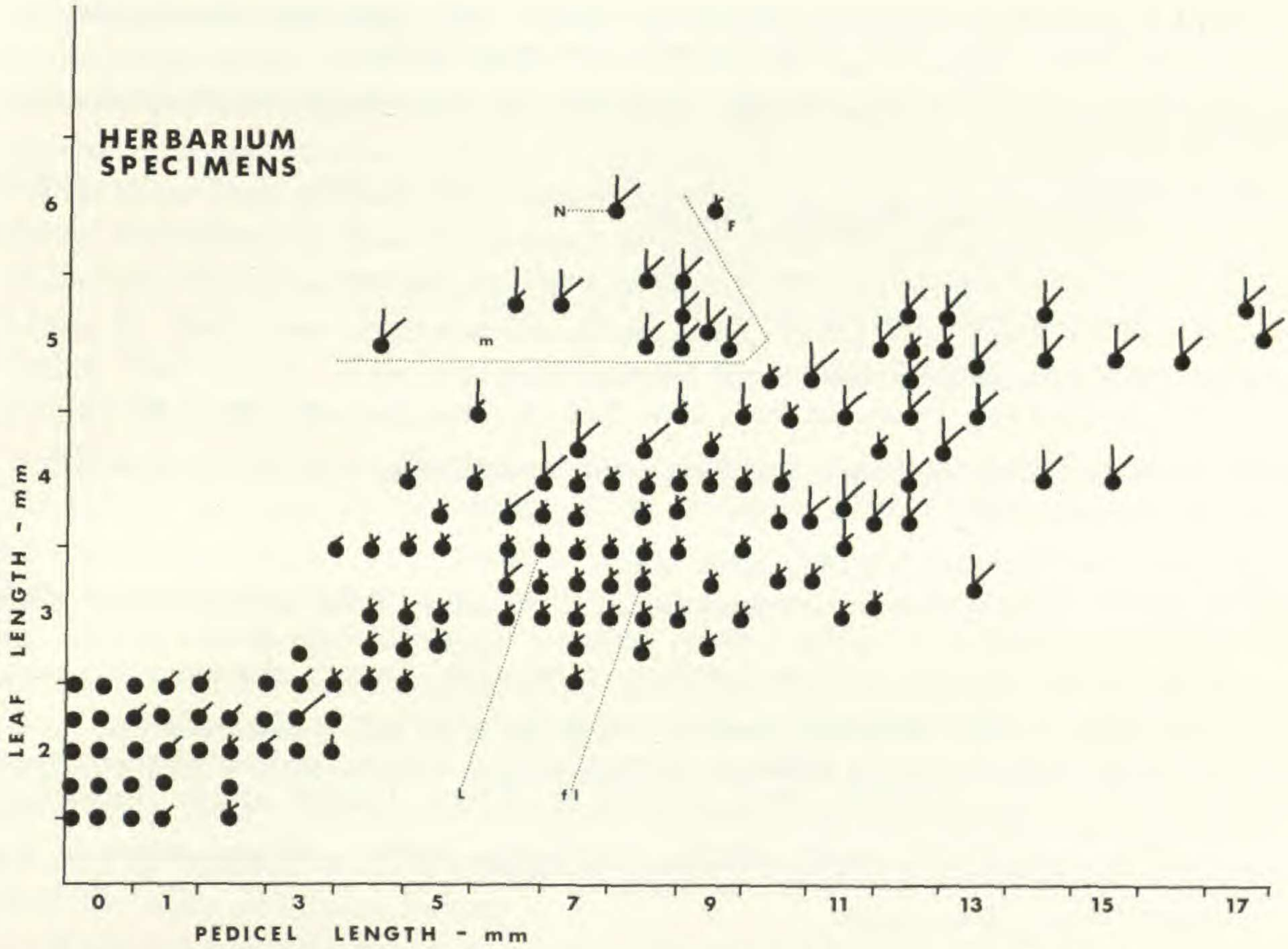

FIGURE 1. — Scatter diagram of four measurements of *Hudsonia* plants from representative herbarium specimens. See upper right of Fig. 2 for explanation of both vertically-oriented and angled bars and half-bars. Glyphs set apart with dotted lines and indicated "m" represent individual subsp. *montana* plants. Single individual marked "N" represents Nuttall's type specimen for his *H. montana*. Individual marked "F" represents plants typical of extant population at Freedom, New Hampshire. Individual marked "L" represents Linnaeus' type specimen of his *H. ericoides*. No data on ovary hairiness were obtained for this specimen. Individual marked "fl" represents Fernald's type specimen of his forma *leucantha*. Glyphs at lower left, with pedicel lengths from 0 to 3 mm and leaf lengths of 2 and 3 mm represent 25 individuals each; all other glyphs represent separate individuals, but were replicated an average of 5 times among the various collections studied. Further explanation in the text.

(Anderson, 1949), here presented as Figure 1. Seed number values were not utilized because of absence of fruiting material on many specimens. The width of the spindle in Figure 1, according to the statistical methods of Kendall (1962) and Goodman (1966) measured within the 99% level of significance. Five extant Massachusetts populations were studied in detail. These populations were located as follows: Plum Island, Crane's Beach, Ipswich, a beach area and an inland area along Cove Road, Wellfleet, and one inland dry, open area near Pine Hill Cemetery, North Truro (Table 3 and Fig. 2). The life histories of these populations were followed over a five-month period (April–August, 1966), and specimens were collected at various intervals. Field plot diagrams were made for comparison of percent cover and plant density. Observable ecological conditions and soils of these and several other populations in Maryland, Massachusetts, New Hampshire, Maine, and Nova Scotia were compared.

TABLE 1. Taxonomic treatment of the genus *Hudsonia*. The genus *Hudsonia* as established by Linnaeus (Mant. Plant., 1767) is based upon his *Hudsonia ericoides*.

Hudsonia ericoides L.

subsp. *ericoides*
(H. *ericoides* L. forma *leucantha* Fernald)

subsp. *tomentosa* (Nutt.) Nickerson & J. Skog comb. et stat. nov.
(*H. tomentosa* Nutt., Gen. N. Amer. Pl. 2: 5. 1818.

subsp. *intermedia* (Peck) Nickerson & J. Skog comb. et stat. nov.
(*H. tomentosa* var. *intermedia* Peck, New York St. Mus. Rep. 45: 86. 1893.

ssp. *montana* (Nutt.) Nickerson & J. Skog comb. et stat. nov.
(*H. montana* Nutt., Gen. N. Amer. Pl. 2: 5. 1818

ssp. *andersonii* Nickerson & J. Skog subsp. nov.

Fruticulus globosus dumosus sempervirens, ad 2 dm altus. *Folia* viridula linearia 3–5.5 mm longa glabrata vel glabra. *Flores* axillares lutei; pedicelli graciles 11–16 mm longi. *Calyx* persistens. *Ovarium* hirtellum vel hirsutum. *Capsula* plerumque trisperma.

Small globose, bushy-branched, evergreen shrub, to 2 dm tall. Leaves greenish, linear, 3–5.5 mm long, glabrate to glabrous. Flowers axillary, yellow; pedicels slender, 11–16 mm long. Calyx persistent. Ovary hirtellus to hirsute. Capsule usually 3-seeded.

Ecological preferences: Shade tolerant; argillaceous shallow soil not subject to sea spray. Known extant population on headlands 30 m above sea level, south shore of Purcell's Cove, Nova Scotia.

Type collection: *Troop 85*, Purcell's Cove, Nova Scotia, August 1966 (GH). Paratype collections: *Nickerson 2908, 2909*, Purcell's Cove, Nova Scotia, August 1968; *Donley 1320*, Queens Co., Nova Scotia, 1958 (ACAD, BH, CONN, DAO, FLAS, MO, NCU, NEBC, NHA, NY, US, and Tufts University). Paratypes from areas with no apparent extant populations: *Redfield 11695*, Martha's Vineyard, Massachusetts, 1885. *10004*, Nantucket Island, Massachusetts, 1885. *Fernald*, Cape Popham, Maine, 1894. *Fernald & Long 9946* (in part) Wareham, Massachusetts, 1913.

RESULTS AND DISCUSSION

The pattern data fall into a spindle which, when measured statistically, is uniform and narrow, indicating that the measured characters are consistently related. Symbols at the left corner of Figure 1 each represent 25 plants, whereas those in the upper right corner represent single plants. These results are interpreted to mean that the measured values for a specific plant are predictable and that influence of one extreme (*Hudsonia ericoides* subsp. *tomentosa*) is predominant in extant seaside populations. Table 1 summarizes the taxonomic treatments for each of the overlapping sub-groups of ecologically and/or geographically distinct major populations.

Measurements from specimens of *Hudsonia montana* Nutt. (here considered as *H. ericoides* subsp. *montana*) were included in the graph (Fig. 1) and marked m, although the living members of this taxon on Table Mountain, North Carolina, now appear to be extinct (personal correspondence, A. E. Radford). Since representatives of this taxon can be plotted almost midway from the extremes found, they may represent a relict population derived from a cross of subsp. *andersonii* (see below) and subsp. *tomentosa*. Possibly because

of post-glacial isolation, the Table Mountain population has remained an intermediate entity in which little selection for the presumably less well-adapted extreme parental types can be detected. Its ecological requirements appear similar to many of the present populations of intermediate forms (Table 2). While these facts indicate that subsp. *montana* can logically be included among subsp. *ericoides*, it is here maintained as a separate taxon because of its probable extinction, its present herbarium documentation, and its prior isolated occurrence. Lewis E. Anderson (personal communication, 1970) has stated to the second author that subsp. *montana* also occurs on a few neighboring hills in the vicinity of Table Mountain.

Measurements of a photograph of Linnaeus' type species, as well as the description he gave in the *Mantissa Plantarum* (1767), indicate that he also was dealing with an intermediate form when he named *Hudsonia ericoides*. This specimen has been seen by the first author in London. According to the 8th Edition of *Gray's Manual* (Fernald, 1950), all similar specimens must be included with *H. ericoides* L., while those tending toward *H. tomentosa* Nutt. must be called *Hudsonia tomentosa* var. *intermedia* Peck. This study presents evidence that a gradation of measurable characters between, among, and beyond these taxa exists and that ecological requirements strengthen our suggested taxonomic separations. The proposed taxonomic revision in Table 1 is consistent with the data discussed below.

Hudsonia ericoides subsp. *tomentosa* (Nutt.) Nickerson & J. Skog is a common and clearly identifiable taxon. It may be regarded as one parental extreme that may have contributed to hybrid populations which have been variously and somewhat arbitrarily set off and designated as separate species.

Hudsonia tomentosa var. *intermedia* Peck must be refined in concept, as must *H. ericoides* L., since these two as well as *H. montana* Nutt. represent intermediate forms. The taxon *H. ericoides* f. *leucantha* Fernald has no valid standing, as we have found single plants with some branches all white-flowered and others all yellow-flowered. The plants now growing at Purcell's Cove, Nova Scotia, and present as at least one specimen from Prince Edward Island, emerge as another taxon as yet unnamed. It is here designated *H. ericoides* L. subsp. *andersonii*, Nickerson & J. Skog in honor of Edgar Anderson, 1896–1969, originator of the method of extrapolated correlates by which the characters of this taxon were first predicted and later verified, first through herbarium records and later in the field (see Anderson, 1949, 1952).

Ecological notes are summarized in Tables 2 and 3. *Hudsonia ericoides* subsp. *tomentosa* requires fine open sand and full sun for optimum growth. The plant is spreading in habit. Well-established individuals are 0.5–2 dm high and 2–6 dm in diameter, but form is influenced by wind, shade, and soil movement onto the site. Along the seashore these plants are first encountered behind the crests of front dunes, sheltered from the brunt of salt and whipped sand, but nonetheless in a habitat to which sand is being intermittently added. The plants may grow close together forming a closed mat over the rolling dune surface (as at Plum Island, Massachusetts), or they may be scattered from 0.5 to 1 meter apart singly over the sand (as at Assateague Island, Maryland).

TABLE 2. Comparison of characters of the subspecies of *Hudsonia ericoides* L.

Taxonomic designation	Pedicel length (mm)	Leaf length (mm)	Leaf hair condition	Ovary condition	Average number of full-formed seeds per fruit	Habit	Shade tolerance	Soil preference
subsp. *tomentosa* (Nutt.) Nickerson & J. Skog	0–1	1.5–2.5	hirsute	glabrous to glabrate	1	spreading	none	dry sandy reaches
subsp. *intermedia* (Peck) Nickerson & J. Skog	1.5–7	2–3.5	hirsutulous to hirsute	glabrate to hirtellous	1 with 2 partially developed	spreading	none to slight	dry sandy reaches
subsp. *ericoides*	4–10	3–4.5	hirtellous to hirsutulous	hirtellous to hirsutulous	1, sometimes 2; with 2 or 1 partially developed	subglobose	none to considerable	dry sand-clay mixtures
subsp. *montana* (Nutt.) Nickerson & J. Skog	4–7	5–6	glabrate	hirsute	(undetermined) reported by Nuttall as 1	subglobose	(unknown)	weathered rock soils
subsp. *andersonii* Nickerson & J. Skog	11–16	3.–5.5	glabrate to glabrous	hirtellous to hirsute	3	globose	high	argillaceous soils

TABLE 3. Comparison of development in three subspecies of *Hudsonia tomentosa* from several localities in eastern Massachusetts, 1966 growing season. (Pattern verified again by N. H. N. in 1970, but flowering periods 5 days later).

Date	subsp. *tomentosa*	subsp. *intermedia*	subsp. *ericoides*
May 4	no growth noted	no growth noted	few early flowers open
May 25	no growth noted	few early flowers open	peak of flowering
June 1	few early flowers open	peak of flowering	end of flowering
June 2–3	peak of flowering	end of flowering	maturing fruits
June 4	end of flowering	maturing fruits	active vegetative growth
June 20	maturing fruits, active vegetative growth	active vegetative growth	fruits falling
July 4	maturing fruits, active vegetative growth	fruits falling	new growth, hardening[a]
July 20	fruits falling	new growth, hardening[a]	
August 10	new growth, hardening[a]		

[a] Vegetative growth may cease in midsummer or may apparently continue slowly into October, depending on rainfall pattern and Indian summer weather.

This distribution may be a reflection of the age of the stand, older plants apparently being more scattered. Subspecies *tomentosa* is gradually invaded by other sand-dune species and is spoken of as "growing in open association" with beach plum (*Prunus maritima*), bayberry (*Myrica pennsylvanica*), beach grass (*Ammophila breviligulata*), pine (*Pinus rigida* or *P. taeda* southward), poison ivy (*Toxicodendron radicans*), seaside goldenrod (*Solidago sempervirens*), several species of *Lechea*, and beach pea (*Lathyrus japonica*). It apparently does not thrive nor long persist in the shade of other plants. Blowing sand may cover most of a plant; however, if the tips remain above ground, they will both flower and continue vegetative growth. These extensive root and branch systems apparently contribute to dune stabilization. This subspecies follows beach grass on the dunes in succession; however, it is not as resistant to abrasion and does not colonize the foot paths or vehicle tracks of man. The plants also do not grow on dry narrow dune crests nor in the low, wet, and boggy ("black water") areas often found among dunes. It is this subspecies which ranges along the coast from the tip of the Gaspé peninsula to the Outer Banks of North Carolina, westward on sandy blowouts to West Virginia and the Great Lakes region in the United States, and as far west as Alberta in Canada. It is least variable at its extremities, based on our studies of both living plants and preserved specimens.

Hudsonia ericoides subsp. *andersonii* was found only in shallow argillaceous soils (those with a noticeable percentage of clay). These soils occur over acidic rock bases, and as a stable product of weathering, they are rather different from the constantly shifting sandy soils of dunes. Typical plants of subsp. *andersonii* are 1–2 dm high, densely branched, spherical, and upright, rather than open, low, spreading, and sprawling as are those of subsp. *tomentosa*. In the barren rocky fields along Purcell's Cove, Nova Scotia, subsp. *andersonii*

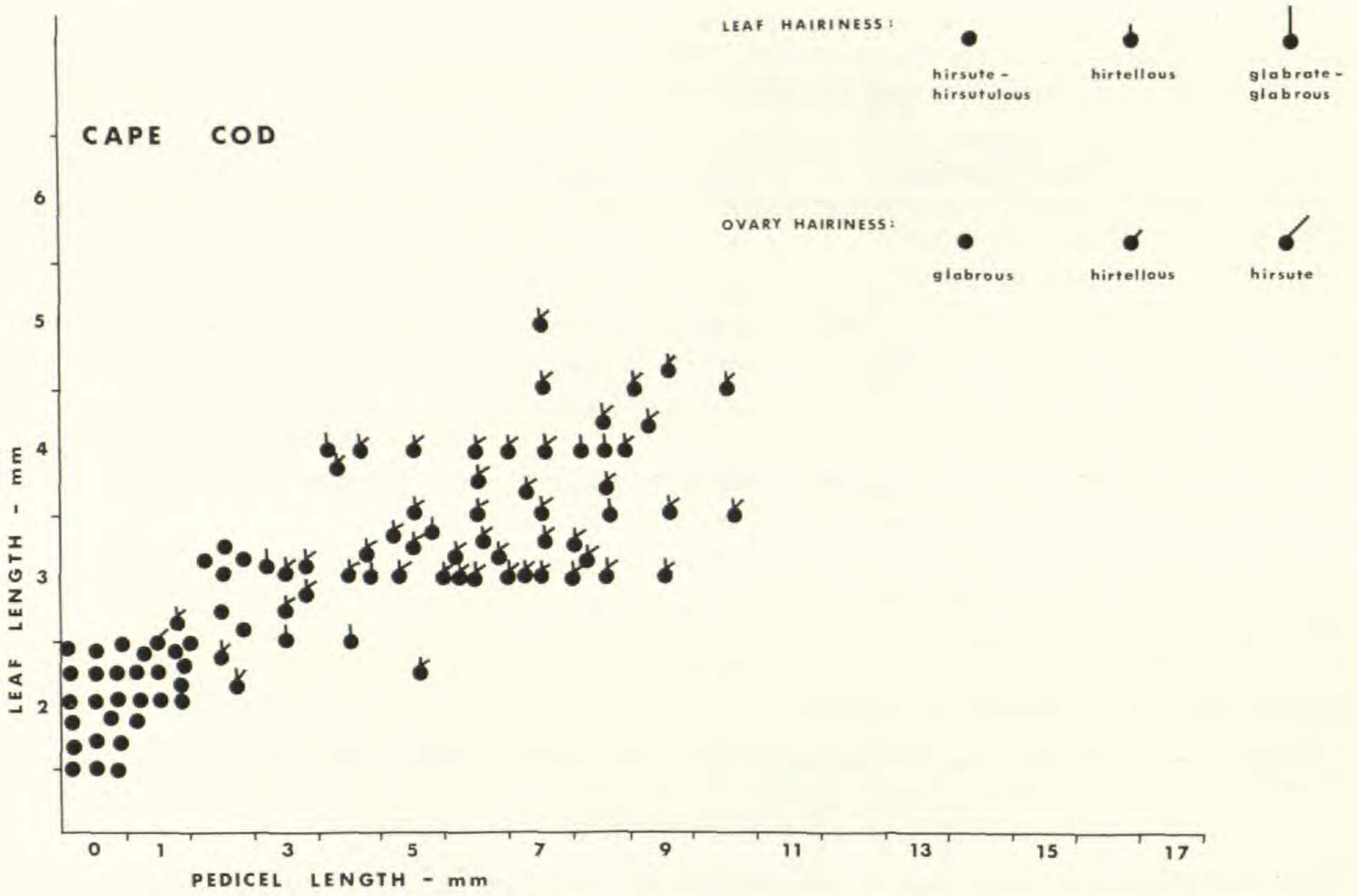

FIGURE 2. — Scatter diagram of four measurements of *Hudsonia* plants collected for study from representative extant populations on Cape Cod. Explanation of both vertically-oriented and angled half-bars in upper right. Glyphs at lower left, with leaf lengths of 2 and 3 mm and pedicel lengths from 0 and 3 mm represent 25 individuals each; all other glyphs represent separate plants whose frequency of occurrence on the peninsula as a whole is much lower. Note that glyphs clearly indicating either subspecies *andersonii* or *montana* are lacking. Further explanation in the text.

individuals dot the landscape and are in association with mosses, lichens, lycopods, several species of *Vaccinium*, and pine sprouts. Root systems are not as extensive nor as deep as those of subsp. *tomentosa*. Subspecies *andersonii* apparently can persist in partial shade; in the areas where it is now found, many of the plants are shaded for several hours of each day. While at least one individual from Prince Edward Island occurred among the herbarium specimens, it is not known if that population is extant.

Intermediate forms (subsp. *intermedia* and subsp. *ericoides*) may grow in fine sand, in clay and gravel, or most commonly in mixtures of sand, clay and gravel (*cf.* Anderson, 1949). The plants have either a rounded or spreading form with extensive root systems, but not quite as extensive as those characteristics of subsp. *tomentosa*. Bushy intermediate plants (those resembling subsp. *andersonii* most strongly) can stand partial shade and on Cape Cod grow in association with blueberry (*Vaccinium angustifolium*), broom crowberry (*Corema conradii*), bearberry (*Arctostaphylos uva-ursi*), and pitch pine (*Pinus rigida*). Certain observations of developmental histories of the three plant taxa common to Massachusetts are summarized in Table 3. The dates of flowering show that cross pollination between taxa can occur, but that they tend to remain intra- rather than inter-fertile.

Distribution of *Hudsonia* subspecies on the outer part of Cape Cod was carefully noted. A local Wellfleet resident informed us that some areas of the high plains of Truro and Wellfleet, originally forested, were logged and used for pasture and agriculture. Now pitch pines are taking over these fields. Subspecies *intermedia* is present over much of the Cape in sandy seaside areas, but there is a noticeable lack of all *Hudsonia* plants along the beaches of the heavily-used south shore from Falmouth to Chatham. An exception occurs at West Dennis, where several dozen plants of subsp. *tomentosa* have appeared in a dune area fenced off for four years. Subspecies *andersonii* is no longer found on Cape Cod; the intermediate forms closest to it occur sporadically inward from the shore on the almost untraveled, sparsely forested, rolling hills of the lower Cape from Wellfleet to Provincetown. These intermediate forms range from "good" subsp. *ericoides* inland to "good" subsp. *intermedia* nearer the outer dunes. Vegetation at the Marconi Beach and Headquarters areas of the Cape Cod National Seashore is particularly rich in such forms and shows the gradation clearly in both flowering dates and vegetative characters. When a new area is opened, such as the open sandy barrens beside modern stores on Route 6 in Wellfleet and the banks of the highway rotary at the terminus of U. S. Route 6 in Provincetown, variable forms resembling either one of both extremes appear, in about equal proportions, perhaps because stray deposits of sand-clay road base soil lie in close proximity with dune sand (*cf.* Anderson, 1948). In mixed populations of this type there is much variation, consistent within each plant, in lengths of all four characters used in Figure 1 and in general plant form. These groups are here regarded as intermediates, and all may be separated out as either subsp. *intermedia* or subsp. *ericoides*, as defined in Table 2.

Geographical distribution in the United States and Canada from north to south and east to west is presented in Table 4, which summarizes information from field work and from herbarium specimens.

These data indicate that the intermediate forms which are here treated taxonomically as subsp. *intermedia* and subsp. *ericoides* are far more common than the extreme subsp. *tomentosa* and subsp. *andersonii*, most probably because disturbed habitats formed and maintained by man's activities abound. Examples of such are mowed and brushed roadsides, fields, railroad embankments and rights of way, abandoned sand pits, and new sandy road cuts and fills. Individuals of subsp. *tomentosa* seem to be confined to undisturbed open dunes and sand banks. This subspecies is not highly variable, but a greater number of intermediate individuals more closely resemble this parental type, possibly because they have derived from it a greater tolerance to open, dry, dune-like areas where competition from other vegetation is at a minimum and where the more than occasional passage of man contributes to continued habitat disturbance. The higher headlands and open savanna-like evergreen tree-shrub habitats which have some clay in their soils were apparently the original habitats of subsp. *andersonii*. These areas, since the advent of man, have become much more severely altered in their vegetational cover than have the dunes. They were utilized by man successively for timber cutting, pastures, and farmlands,

TABLE 4. Geographical distribution (from collections and annotated herbarium specimens).

Location by state or province	subsp. *tomentosa*	subsp. *intermedia*	subsp. *ericoides*	subsp. *montana*	subsp. *andersonii*
Nova Scotia	×	×	×		×
Newfoundland	×	×			
New Brunswick	×				
Prince Edward Island	×	×	×		×[a]
Quebec	×	×	×		
Maine	×	×	×		×[a]
New Hampshire	×	×	×		
Vermont	×				
Massachusetts	×	×	×		×[a]
Rhode Island	×				
Connecticut	×	×			
New York	×	×			
New Jersey	×	×	×		
Maryland	×				
Delaware	×	×			
Virginia	×				
North Carolina	×			×	
West Virginia	×				
Ohio	×				
Indiana	×				
Illinois	×				
Michigan	×				
Iowa	×				
Wisconsin	×				
Minnesota	×				
Ontario	×				
Manitoba	×				
Saskatchewan	×				
Alberta	×				

[a] Population probably not extant.

and they now are being cut up for building lots. Because of man's unchecked uses of this habitat in Nova Scotia, we conclude that subsp. *andersonii* is disappearing there, and intermediates which resemble it, confined as they are by selection to the same areas desired by man for other uses, will become far less frequent in the total population of *Hudsonia*. We presume that this situation is being intensified because subsp. *ericoides* is no longer as wide-spread as herbarium specimens indicate it once was. Indeed, Nuttall (1818) stated "*ericoides*" to be along the "Virginia, New Jersey and North Carolina coasts."

Our evidence is strengthened by recent collections of subsp. *andersonii* having been made only from an active subdivision area at Purcell's Cove, Nova Scotia, and intermediate plants resembling it being markedly less frequent in occurrence, both now and in herbaria, than those resembling subsp. *tomentosa*.

In some areas (the beach at Ogunquit, Maine; Plum Island, and Crane's Beach, north of Boston, beaches at Sagamore and at Chapin Memorial Beach in Dennis, on Cape Cod, all in Massachusetts) no subsp. *andersonii*-like forms (here considered as subsp. *ericoides*) exist at all, yet there are herbarium records of their collection from these locations. A "rare find" (personal communication, Frank McKeever) collected in New Jersey in 1966 and sent to the second author turned out to be an intermediate form which would be classified here as subsp. *ericoides*. There is a 1960 collection of one plant from New Jersey which also is so classified. Subspecies *ericoides* also presently exists on Nantucket, Martha's Vineyard, in Provincetown, Truro, Wellfleet, the south side of Dennis, and Plymouth, Massachusetts, as well as in isolated coastal areas of Maine, Prince Edward Island, Nova Scotia, and New Brunswick, and inland at Freedom, New Hampshire (see Fig. 1).

Hall (1956) stated that his data indicated perhaps a considerable time period had been involved in the production of all these intermediates (referred by him to var. *intermedia* Peck). It has been certainly implied in our data that this spread of characters represents the development of hybrids from two parental types and may indeed be leading to introgression in the sense often proposed by Anderson (1949), which is that variation in the parental types is gradually increasing by backcrosses with the presumptive hybrid swarms. In view of the evidence recently presented by Randolph *et al.* (1967) that the original species of *Iris* studied by Anderson and Riley (Anderson, 1949) are still very much extant and seem to be unchanged, and of Rudloff *et al.* (1967) and of Flake *et al.* (1969) regarding the apparent lack of introgression in *Juniperus*, it may be premature to indicate that introgression in any sense has occurred in *Hudsonia*. It seems reasonable to interpret our data as meaning that two new complexes of characters, clustering around subsp. *intermedia* and around subsp. *ericoides-montana* as herein defined, are emerging from a much broader spectrum in the genus *Hudsonia*, and that the extremes of this spectrum, represented by subsp. *tomentosa* and subsp. *andersonii*, may be facing extinction because of subtle but relentless pressures imposed by increased populations of man. However, two further interpretations are possible. We may be dealing with a single clinal variation, as has been proposed in *Juniperus virginiana* (Rudloff *et al.*, 1967; Flake *et al.*, 1969). Alternatively, we may be dealing with two clinal variations, one *tomentosa-intermedia*, the other *ericoides-montana-andersonii*, neither one particularly involved in gene exchange with the other. To help resolve these questions, a study of biochemical constituents of extreme plants and several of their intermediates is now being conducted in another laboratory, utilizing modern chemotaxonomic methods. These results will be presented in a subsequent paper.

Pollen studies made with the light microscope do not reveal any easily-discernible consistent morphological differences. Pollen from both fresh and preserved specimens were compared. Electron scanning microscope studies are currently underway by John Semple, Missouri Botanical Garden, to confirm or deny this sameness.

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